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HANDLING TIME AND CHOICE IN PIGEONS

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According to optimal foraging theory, animals should prefer food items with the highest ratios of energy intake to handling time. When single items have negligible handling times, one large item should be preferred to a collection of small ones of equivalent total weight. However, when pigeons were offered such a choice on equal concurrent variable-interval schedules in a shuttlebox, they preferred the side offering many small items per reinforcement to that offering one or a few relatively large items. This preference was still evident on concurrent fixed-cumulative-duration schedules in which choosing the alternative with longer handling time substantially lowered the rate of food intake.

Key words: concurrent schedules, reinforcement magnitude, reinforcement delay, handling time, foraging, shuttlebox, pigeons

According to optimal foraging theory (Krebs, Stephens, & Sutherland, 1983; Pyke, Pulliam, & Charnov, 1977), animals should have behavioral mechanisms that allow them to maximize energy intake per unit spent foraging (E/T). This means, among other things, that foragers should select food items with the highest ratio of energy yield to handling time (E/h) or profitability. Handling time is the time necessary to pursue, prepare, and consume an item, time during which the forager cannot search for other items.

The range of items it is optimal to select depends on the relative availability of the more profitable ones. When profitable items are sufficiently abundant, less profitable items should be rejected; as the abundance of the more profitable items declines, less profitable items should be added to the diet in order of profitability in an all-or-nothing manner. This prediction of optimal foraging theory has been qualitatively but not always quantitatively confirmed in a number of studies with predators feeding on their natural prey (e.g., Krebs et al., 1983; Lea, 1981).

Interest in relationships between foraging theory and behavior in schedules of reinforcement has generated several experiments with pigeons in which the problem of item selection has been simulated with reinforcement schedules in a conditioning chamber. Different colors on the pecking key correspond to different items, and their profitability can be varied by varying the signaled delay to reinforcers of fixed size (Abarca & Fantino, 1982; Lea, 1979) or by varying the magnitude of reinforcement available within a constant "handling time" (Snyderman, 1983). In such studies, handling time is simulated by a prefood delay during which the pigeon must wait to eat and cannot work for other items. The situation is formally similar to that confronted by a bird cracking a seed or killing an insect: The item is at hand but cannot yet be consumed. However, this is not a realistic simulation of situations that commonly confront pigeons and other granivorous birds when they feed on seeds and other small items that can be snapped up quickly. Such items vary not in handling time but in energy value, which corresponds roughly to size. The bird can obtain the same amount of food by pecking once and getting one large item or by pecking many times and getting many small items. When large items are suffi-

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ciently abundant, an animal in this sort of foraging situation should select large items over small ones, and it should select one large item over a collection of many small ones.

Animals of many species do prefer large items to small (Krebs et al., 1983; Lea, 1981), but pigeons do not appear to share this preference. In studies in which pigeons have been allowed to feed on a variety of items, they have usually been found to have idiosyncratic preferences, some eating more large items like corn and peas, others eating more small ones like hemp and millet (Brown, 1969; Moon & Zeigler, 1979). Moon and Zeigler's data do show, however, that hungry pigeons consume most of the peas (i.e., relatively large items) they take at the beginning of a bout of feeding; this observation is consistent with the notion that animals are more selective when they are feeding at high rates, and sample less profitable items at other times (Christensen-Szalanski, Goldberg, Anderson, & Mitchell, 1980). Although pigeons' individual variations in preference have not been accounted for, it is perhaps not surprising that when items vary in shape, hardness, composition, and appearance, size is not the only determinant of choice. In addition, the item-selection problem usually dealt with in foraging theory involves successive encounters with single items, rather than simultaneous presence of many items. However, it seems clear that with a constant short handling time, as with seeds for a pigeon, E/T would be maximized by selecting large items. And of course when dealing with different kinds of food items, it must be remembered that the notion that fitness is maximized when energy intake is maximized, regardless of nutrients, is an admitted oversimplification (Krebs et al., 1983).

Conventional studies of the effects of reinforcer magnitude on pigeons' choice provide little information about the effects of the various determinants of profitability on choice. Reinforcement magnitude has usually been measured as duration of food-hopper presentation; as a result, time spent feeding and amount consumed are usually confounded. There is some evidence that granivorous birds assess amount eaten by a rule of thumb (Krebs et al., 1983): "More pecking is more food." Wolfe and Kaplon (1941) trained domestic chicks in a runway with reinforcers consisting of one whole grain of corn, one quarter grain of corn, or four quarter grains of corn. One whole grain generated better performance than one quarter grain, but four quarter grains generated much better performance than one whole grain.

Such effects appear to be fairly general. For example, Hall and Kling (1960) gave rats in a T maze a constant number of drops of sucrose in few or many cups. The rats learned more rapidly under conditions offering more consummatory activity, to the point where six drops of sucrose in six cups was a better reinforcer than twelve drops in two cups. Similarly, children shown identical amounts of liquid distributed in two or six beakers display Piagetian failure of conservation and judge that the six beakers offer more to drink (Bruner, 1966).

Results like those of Wolfe and Kaplon and of Hall and Kling (see Bolles, 1967, for a review of others) lend support to consummatory-response theories of reinforcement. At the same time, however, in experiments that compare the same reinforcer in different numbers of pieces or containers, visual extent of the reinforcer may be important independently of how much of the reinforcer the animal is allowed to consume (e.g., Dyal, 1960). More recent work suggests that such effects are better interpreted as showing that animals return more readily to undepleted than to depleted food sources and that visual extent of food originally at the goal is unimportant (Gaffan, Hansel, & Smith, 1983). In experiments more closely related to the present ones, Yoshioka (1930) showed that rats preferred large sunflower seeds to small ones even though the seeds with larger shells had the same sized kernels and took longer to eat. Yoshioka concluded that the rats were fooled by the visual size of the seeds, but the fact the larger seeds required longer to shell (i.e., afforded more consummatory activity) may also have been a factor.

In the present studies, pigeons were offered choices between obtaining one or a few relatively large food items and obtaining many small items of the same total weight. Inasmuch as all items had the same composition (they were food pellets of different sizes), from the point of view of optimal foraging theory the choice involved obtaining equivalent energy values with short or long handling times. Would pigeons choose the alternative offering shorter handling times, or would they behave like Wolfe and Kaplon's chicks and choose the alternative that appeared larger and offered more pecking? Although the literature referred to above clearly predicts the latter outcome (which was in fact obtained), the present experiments differed from earlier ones in assessing choice in a free-operant situation. Testing birds in continuous sessions allowed the impact of their preferences on rate of energy intake to be measured directly. Also, the subjects were pigeons, which permits the results of these tests of choice with real food items to be compared in detail to the growing number of studies of pigeons' choices among "items" on schedules designed to simulate foraging situations.

In the experiments reported here, pigeons chose between spending time in two locations in a shuttlebox like that described by Baum and Rachlin (1969). Food was delivered according to similar schedules in both locations. The first two experiments used concurrent variable-interval (VI) schedules, so that the birds could collect all the food that became available while still demonstrating a preference for one combination of size and number of food pellets over another. Experiment 3 involved a more "realistic" situation. The birds worked on ratio-like schedules in the shuttlebox, so that handling time was actually time lost toward "searching" for the next items. In Experiments 2 and 3 the choices of most interest were between one 300-mg item and fifteen 20-mg items. Experiment 4 was designed to test the generality of the conclusions from those experiments by offering choices involving other sizes and numbers of items on concurrent VI schedules.

The experiments were designed to assess preferences for different forms of the same food. Experiments 1, 2, and 4 differed in an important way from the item-selection problem depicted in foraging theory in that on relatively long VI schedules an animal can collect *all* the food that becomes available by changing sides sufficiently often. At the same time, however, a range of time allocations produces the same overall feeding rate (Houston & McNamara, 1981). The underlying assumption of the present experiments is that any preferences the birds display will be the same ones that govern their choice in a conventional diet-selection problem, where handling time is time lost from searching. Experiment 3 can be viewed as a test of this assumption.

EXPERIMENT 1

Baum and Rachlin (1969) described time allocation on concurrent schedules in a shuttlebox with different frequencies of reinforcement at the two ends. The present studies, however, were designed to investigate effects of the rate or manner in which reinforcers could be consumed once they were made available, rather than effects of reinforcement frequency per se. Because there appears to have been no research using time allocation in a shuttlebox to measure the effects of similar variables, a preliminary experiment was designed to measure the effects of signaled delay of reinforcement on choice in concurrent VI schedules in the shuttlebox. As mentioned earlier, this well-studied variable is at least formally similar to handling time. The effects of manipulating delay might therefore be expected to indicate the sensitivity of behavior in the shuttlebox to variables of this kind.

METHOD

Subjects

Five experimentally naive White King pigeons between 6 and 12 months old, from Palmetto Pigeon Plant, were maintained at 85% of their free-feeding body weights.

Apparatus

The experimental chamber was similar to that described by Baum and Rachlin (1969). It was 23 cm high, 22 cm wide, and 62 cm long. The grid floor consisted of two sections, each pivoted at the middle of the chamber and suspended by a spring at the end of the chamber. When the bird stood on one side, the floor on that side depressed a microswitch. Above the translucent Plexiglas ceiling of the chamber were a red light on the right, a green light on the left, and a white light in the center. Centered at each end of the chamber was an opening 6.5 cm wide by 10 cm high by 8 cm deep with its bottom approximately level with the floor. A circular hole in the bottom allowed access to 2-cm-diameter food cups in a circular tray that could revolve and make one cup available at a time. The feeder motor ran continuously and provided masking noise in the experimental room. Two lights were correlated with each feeder. A delay light lit a 4.0 by 8.5-cm translucent panel behind the food cup the same color as the ceiling light on that side; a white feeder light was 11 cm above each food cup.

The time a bird spent standing on each side was monitored and the experimental environment was controlled by electromechanical programming equipment until about halfway through the experiment. Then control was transferred to an Apple II® computer interfaced to the chamber with hardware from S & K Computer Products, Toronto, Ontario.

Procedure

The birds were trained to eat Purina Pigeon Chow from both food cups; then they were required to go from end to end of the chamber to obtain food. Then equal variable-interval (VI) schedules were programmed on both sides, starting with VI 30 s. Initially, there was no changeover delay (COD), so that reinforcement could be given immediately when a bird changed sides. The average interval between food deliveries and the COD was gradually increased, and the time the food cup was available per presentation was decreased, until the birds were working on a VI 90-s schedule with a 4-s COD and 3-s feeder time. This preliminary training took about 10 sessions with 40 food presentations per session.

While a bird depressed the microswitch on a given side, only the ceiling light on that side was illuminated and food was available only on that side. Presentation of the food cup was accompanied by illumination of the white light above it. The ceiling lights were off at that time. Time on a given side was counted only while the ceiling light on that side was lit. The COD began when the pigeon left the side it had just been on. During the COD the white center ceiling light was on and no food could be delivered. The COD ended after the programmed number of seconds if the pigeon was depressing only one side at that time. If neither or both sides were depressed (i.e., the pigeon was in the middle of the box), the COD continued until only one side was depressed. Reinforcers were programmed on independent VI schedules with intervals derived from the formula of Fleshler and Hoffman (1962). In the latter, computer-controlled phases of the experiment, a new random sequence of intervals was arranged for each side on each day. When a reinforcer was programmed, the real or simulated programming tape stopped until the end of the time when that reinforcer has been delivered. Throughout this experiment, each reinforcer consisted of several pieces of Purina Pigeon Chow, and sessions lasted until 40 reinforcers had been presented.

The sequence of conditions to which each bird was exposed after its preliminary training can be seen in Table 1. Between the initial condition, with no delays, and exposure to conditions involving delays, there were five sessions with gradually increasing equal signaled delays on both sides, terminating with 4-s delays. When delayed reinforcement was to be delivered, the panel behind the food cup lit up and the ceiling light went off. The delay light went off at the end of the programmed delay and the feeder advanced. Once it started, the delay and feeder cycle continued regardless of where the bird went in the chamber.

Following the preliminary exposure to equal delays, all birds had 4-s delay on their less preferred side versus no delay on the other; 8-s delay on this same side versus no delay; and finally 8 versus 0 s with the delayed side reversed. The basic schedule remained VI 90 s throughout this phase. A final series of sessions with no delay was run at VI 60 s, except in the case of Bird 1, who had fallen behind the

Table 1

Means based on the last 3 days per condition in Experiment 1. Conditions are listed for each bird in the order run. Time in changeover includes the COD (4 s) plus any additional time the bird spent in the center of the shuttlebox after leaving one side before moving onto the other. Times on each side exclude feeder times.

		Delay (s)		*Time (s)*		*Reinforcements*		*Changeovers*		*Relative reinforcers left*	*Relative time left*
Condition	*Days*	*Left*	*Right*	*Left*	*Right*	*Left*	*Right*	*No.*	*Time (s)*		
Bird 1											
0-90	10	0	0	327.6	370.7	20.3	19.6	219	971.4	.509	.468
4R	10	0	4	258.6	285.9	19.0	21.0	261	1102.6	.475	.477
8R	15	0	8	263.5	158.8	20.0	20.0	310	1271.9	.500	.626
8L	10	8	0	154.9	177.0	19.6	20.3	323	1297.8	.491	.465
Bird 2											
0-90	10	0	0	340.2	329.4	20.3	19.6	236	1031.8	.509	.507
4R	10	0	4	338.6	325.2	21.6	18.3	241	1088.8	.542	.502
8R	15	0	8	279.2	335.4	22.0	18.0	252	1099.3	.550	.454
8L	15	8	0	251.9	488.5	17.6	22.3	263	1079.6	.441	.348
0-60	10	0	0	210.5	199.7	20.3	19.6	194	782.5	.509	.513
Bird 5											
0-90	10	0	0	372.9	328.1	19.6	20.3	249	1078.2	.491	.531
4L	10	4	0	295.8	293.2	22.3	17.6	231	977.3	.558	.501
8L	15	8	0	177.9	328.4	19.6	20.3	310	1254.8		
8R	15	0	8	234.7	250.6	18.0	22.0	323	1349.4	.450	.482
0-60	10	0	0	195.7	167.3	18.6	21.3	247	998.5	.466	.409
Bird 9											
0-90	10	0	0	327.3	324.1	20.3	19.6	235	1071.1	.509	.503
4R	10	0	4	338.7	301.0	19.6	20.3	225	1034.8	.492	.530
8R	15	0	8	262.2	274.2	20.6	19.3	238	1019.2	.517	.489
8L	15	8	0	170.8	249.1	18.6	21.3	331	1422.9	.466	.406
0-60	10	0	0	117.2	157.9	21.0	19.0	238	954.2	.525	.427
Bird 10											
0-90	10	0	0	274.8	264.2	20.3	19.6	256	1104.8	.508	.510
4L	10	4	0	252.6	312.7	18.6	21.3	267	1183.6	.466	.445
8L	15	8	0	184.5	349.8	20.3	19.6	280	1188.8	.508	.346
8R	15	0	8	355.8	228.5	20.3	19.6	309	1260.9	.509	.609
0-60	10	0	0	157.4	144.9	19.0	21.0	241	968.0	.475	.521

others because of frequently being overweight. In each condition, all birds were run for the same number of sessions (see Table 1). Sessions were run 5 days a week.

RESULTS AND DISCUSSION

The 4-s signaled delay had relatively little effect on choice; the 8-s delay had a consistent but small effect (Figure 1). Unlike the case in Baum and Rachlin's (1969) experiments, the pigeons had no consistent bias toward one side of the shuttlebox when reinforcement contingencies were the same on both sides, in the first and last conditions. Three of the 5 birds slightly decreased their relative times on their initially favored side when the 4-s delay was introduced there. When the delay on that side was increased to 8 s, 4 of the pigeons markedly decreased their relative times on the side with a delay. When the 8-s delay was shifted to the opposite side, all 5 birds increased their relative times on the side that now had zero delay.

Throughout, relative times changed with changes in the side offering delayed reinforcers; the proportion of reinforcers obtained on each side remained around 50%. This result can be seen most clearly in the group data in Figure 1. It means that changes in relative times on the two sides are not simply a case of matching relative times to relative numbers of reinforcers obtained, but rather are an effect of delay per se.

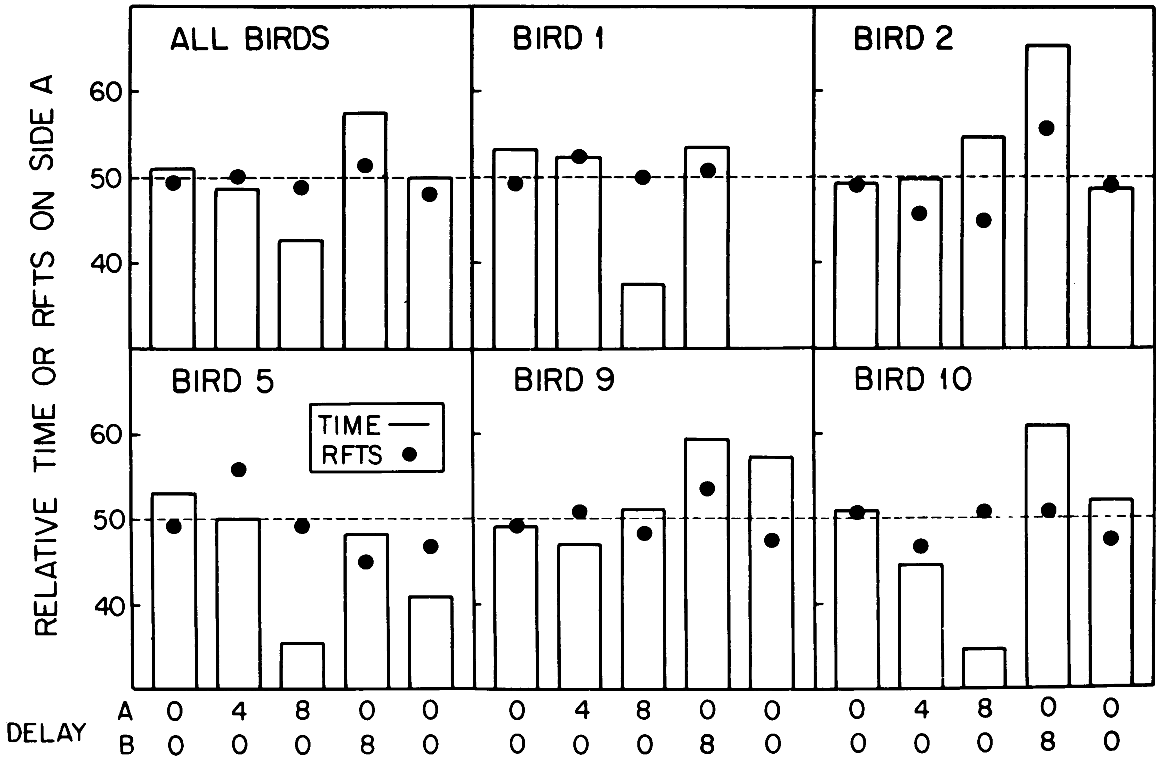

Fig. 1. Mean percentage of time spent and reinforcers obtained on the side where delay was first introduced, "Side A," during the last 3 days of each condition in Experiment 1.

Studies of delayed reinforcement of key pecking on VI schedules (e.g., Chung, 1965; Chung & Herrnstein, 1967; Marcattilio & Richards, 1981; Richards, 1981) suggest that pigeons should display a preference for no delay over 4- or 8-s delays on concurrent VI schedules. However, variables like the lengths of the basic VI and the COD and the nature of the delay signal, if any, would all be expected to influence the degree to which preference for a shorter delay is exhibited on such schedules. For that reason, the present data cannot be compared in detail to those of previous experiments. For example, using VI 1 min, a 1-s COD, a blackout during the delay, and equivalent blackouts unrelated to food in the zero-delay component, Chung (1965) found relative responding for 8-s as opposed to 0-s delayed reinforcement reduced to 20% of total responding. The effect of 8-s delay was much less evident in the present experiment, possibly because of the longer VI, the longer COD, and/or the use of a discrete signal near the food source rather than a blackout during the delay. When differences like these are taken into account, it seems likely that the effects of reinforcement delay in the shuttlebox are comparable to those in key-pecking situations. However, because the effects of even 8-s delay were quite small in some cases here, the basic VI schedule was changed to VI 60 s in the next experiment in the hope of enhancing the display of preference (cf. Marcattilio & Richards, 1981).

EXPERIMENT 2

In this experiment, as in the first one, pigeons were exposed to equal VI schedules on the two sides of the shuttlebox. Here the sides differed in the sizes and numbers of items offered at each reinforcement opportunity. The items were approximately spherical pellets of pigeon food weighing either 300 mg or 20 mg; their maximum dimensions were, respectively, 7.5 mm by 7.5 mm and 3.2 mm by 2.5 mm.

Table 2

Numbers and sizes of food pellets offered per reinforcement, and time for which they were available (feeder time or "handling time") in each condition of Experiment 2.

	Left		Right	
Condition	*Pellet no. & Size*	*Feeder time (s)*	*Pellet no. & Size*	*Feeder time (s)*
1	15 × 20 mg[a] 1 × 300 mg	8.0	15 × 20 mg 1 × 300 mg	8.0
2	1 × 300 mg	1.5	15 × 20 mg	8.0
3	15 × 20 mg	8.0	1 × 300 mg	1.5
4	1 × 20 mg	1.5	1 × 300 mg	1.5
5	1 × 300 mg	1.5	1 × 20 mg	1.5
6	1 × 20 mg	1.5	15 × 20 mg	8.0
7	15 × 20 mg	8.0	1 × 20 mg	1.5
8	1 × 300 mg	8.0	15 × 20 mg	8.0
9	15 × 20 mg	8.0	1 × 300 mg	8.0

[a] These occurred in alternate food cups on both sides.

The larger items resembled good-sized peas. The choice of most interest was that between a schedule offering a single 300-mg pellet and one offering fifteen 20-mg pellets. This condition was run both with equal feeder times, or handling times, for both item types and, in a more realistic manner, with unequal feeder times, just long enough for the 1 large or the 15 small items to be collected. Several control conditions assessed degrees of preference for the different-sized items with number constant or for different numbers with size constant.

METHOD

Subjects and Apparatus

The subjects and apparatus were the same as those in Experiment 1. A computer controlled the events and recorded the data throughout this and the remaining experiments.

Procedure

Throughout this experiment, independent VI 60-s schedules were in effect on the two sides of the shuttlebox. Reinforcers consisted of 300-mg or 20-mg Noyes pigeon pellets. Preliminary observations indicated that a 1.5-s programmed feeder time allowed the pigeons to detect the presence of the food cup and to collect one pellet on most occasions; programming an 8-s feeder time usually allowed fifteen 20-mg pellets to be collected with little time to spare. Therefore, except in various control conditions to be described, these feeder times were used with 1 or 15 pellets, respectively.

A minor difference from Experiment 1 was that the COD began with depression of the side opposite to that which the pigeon had just been on. This eliminated the possibility that a COD could start when a pigeon bounced on one side of the shuttlebox without actually crossing to the other side. The COD was also reduced to 3 s. In all other respects the procedure was the same as that for Experiment 1.

The experimental conditions and the sequences in which individual birds were exposed to them are listed in Table 2. The first condition exposed the birds to equal frequencies of 1 large (300-mg) and 15 small (20-mg) pellets on both sides of the chamber. Subsequently, for each combination of "handling time" and pellet size and number, a given condition occurred on the left and on the right in successive blocks of sessions. Most conditions were run for 10 days, inasmuch as changes in the preferred side between conditions were apparent within one or two sessions and were relatively stable after about five sessions.

RESULTS AND DISCUSSION

All 5 pigeons tended to prefer the side offering 15 small pellets per reinforcement to the one offering 1 large pellet of the same total weight. With 8-s handling times on both sides, all birds spent more than 50% of their time on the side offering 15 small items (Conditions 8 and 9 in Table 3; right-most bar of each panel in Figure 2). In Conditions 2 and 3, the differ-

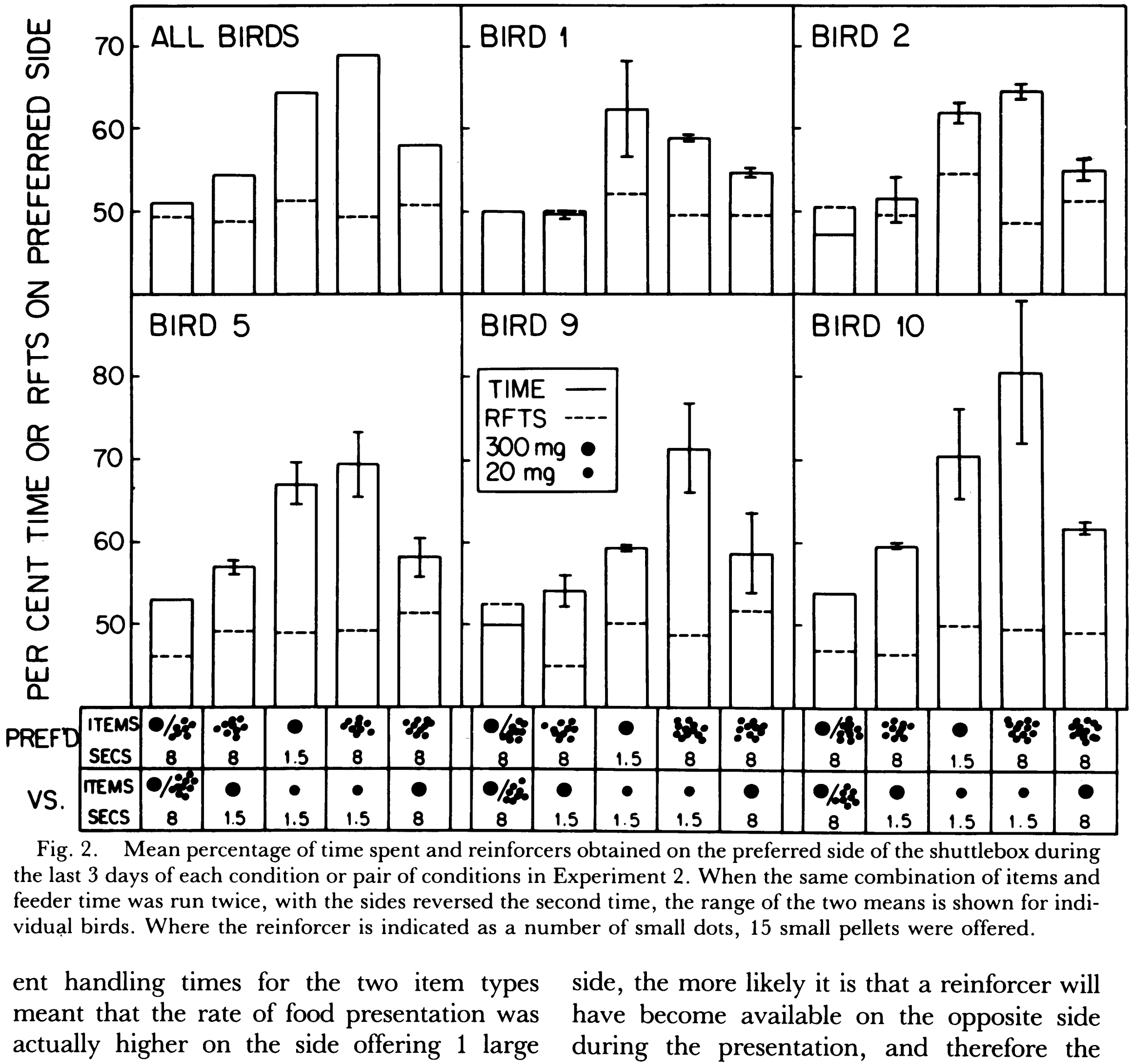

Fig. 2. Mean percentage of time spent and reinforcers obtained on the preferred side of the shuttlebox during the last 3 days of each condition or pair of conditions in Experiment 2. When the same combination of items and feeder time was run twice, with the sides reversed the second time, the range of the two means is shown for individual birds. Where the reinforcer is indicated as a number of small dots, 15 small pellets were offered.

ent handling times for the two item types meant that the rate of food presentation was actually higher on the side offering 1 large item. In these conditions, preference for 15 small items was still apparent but less pronounced than in Conditions 8 and 9, with equal handling times on both sides. In the latter two conditions, not only were the VIs equal, but allowing 8-s feeder time for one large item meant that the pigeons experienced a 6 to 7-s delay after each large pellet before the feeder light went off and the VI went back into effect. This postfood delay might be expected to decrease preference for the side offering single large pellets compared to the conditions with 1.5-s feeder time for the same item. Postfood delay can be aversive in itself (e.g., Logan, 1965). In addition, on concurrent VIs the longer the feeder time on a given side, the more likely it is that a reinforcer will have become available on the opposite side during the presentation, and therefore the more likely the bird should be to leave the side with long feeder time immediately after reinforcement. Either or both of these factors—possibly combined with the fact that when feeder times were unequal, reinforcers were slightly more frequent on the side with one large pellet—would tend to produce the observed difference between Conditions 2 and 3 (with unequal feeder times) on the one hand, and Conditions 8 and 9 (with equal feeder times) on the other.

In the conditions offering 20 mg of food on one side of the shuttlebox and 300 mg on the other, the birds invariably spent more time on the side offering 300 mg of food per reinforcement. All except Bird 1 had a stronger

Table 3

Means based on the last three sessions of each condition in Experiment 2. Changeover time includes the COD (3 s) plus any additional time the bird was in the center of the shuttlebox at the end of the COD. Times on the sides exclude feeder times.

			Reinforcements		*Time (s)*		*Visits*		*Mean visit length (s)*		*Changeovers*		*Relative time*
Condition	*Order*	*Days*	*Left*	*Right*	*Left*	*Right*	*Left*	*Right*	*Left*	*Right*	*No.*	*Time (s)*	*left*
Bird 1													
1	1	10	20	20	140	140	118	135	1.2	1.0	249	751	.500
2	2	10	20	20	155	156	145	143	1.0	1.1	288	868	.499
3	3	10	20	20	133	138	134	148	1.0	0.9	282	850	.492
4	4	10	19	21	134	175	139	147	0.9	1.2	287	864	.433
5	5	10	21	19	230	107	159	101	1.5	1.0	261	784	.682
6	6	10	19	21	136	191	127	141	1.1	1.4	268	811	.415
7	7	9	18	22	222	153	130	128	1.7	1.2	258	779	.592
8	8	10	19	21	141	171	123	136	1.2	1.3	258	779	.457
9	9	10	19	21	166	133	133	123	1.2	1.1	257	773	.554
Bird 2													
1	1	10	20	20	248	277	100	102	2.5	2.7	201	609	.472
2	2	10	19	21	213	254	113	114	1.9	2.2	228	684	.456
3	3	10	19	21	185	194	106	108	1.8	1.8	214	642	.488
4	4	10	18	22	177	304	112	121	1.6	2.5	234	704	.369
5	5	10	22	18	309	199	121	119	2.6	1.7	241	723	.608
6	6	10	20	20	171	324	117	119	1.8	3.2	197	598	.346
7	7	9	19	21	324	183	101	99	3.2	1.9	201	604	.636
8	8	10	19	21	183	214	101	114	1.8	1.9	215	645	.461
9	9	15	20	20	204	160	121	105	1.7	1.5	226	678	.561
Bird 5													
1	1	10	18	22	215	191	117	118	1.8	1.6	235	719	.529
2	2	10	21	19	179	242	116	119	1.5	2.0	236	710	.424
3	3	10	20	20	210	165	118	114	1.8	1.5	233	706	.560
4	4	10	22	18	172	314	107	110	1.6	2.8	218	658	.354
5	5	13	21	19	423	185	113	109	3.8	1.7	223	672	.695
6	6	10	19	21	104	207	104	114	1.5	2.6	220	441	.346
7	7	10	18	22	396	144	101	90	3.9	1.6	193	580	.733
8	8	10	18	22	156	197	112	124	1.4	1.6	236	709	.442
9	9	10	19	21	237	154	119	112	2.0	1.4	231	694	.605
Bird 9													
1	1	10	21	19	228	263	103	103	2.2	2.6	206	619	.465
2	2	10	21	19	214	274	105	104	2.1	2.6	210	630	.440
3	3	10	18	22	227	207	111	118	2.0	1.8	229	686	.522
4	6	10	19	21	194	281	115	116	1.7	2.4	232	699	.409
5	7	10	19	21	269	185	117	118	2.3	1.6	236	707	.591
6	4	10	20	20	146	482	84	92	1.8	5.3	176	534	.233
7	5	10	19	21	343	175	108	112	3.2	1.6	220	661	.661
8	8	10	19	21	171	200	108	121	1.6	1.6	230	689	.461
9	9	10	20	20	272	153	112	95	2.4	1.6	207	622	.638
Bird 10													
1	1	10	19	21	240	167	128	128	1.9	1.3	256	770	.589
2	2	10	20	20	162	240	112	122	1.5	2.0	235	763	.403
3	3	10	19	21	213	144	127	132	1.7	1.1	258	776	.598
4	6	10	21	19	119	382	80	154	1.5	2.5	235	705	.239
5	7	10	21	19	311	166	120	118	2.6	1.4	239	718	.653
6	4	10	17	23	65	534	43	152	1.5	3.7	194	585	.108
7	5	10	17	23	341	132	126	128	2.7	1.0	253	760	.720
8	8	10	21	19	127	211	85	138	1.5	1.5	224	671	.375
9	9	10	21	19	222	140	119	103	1.8	1.3	222	665	.613

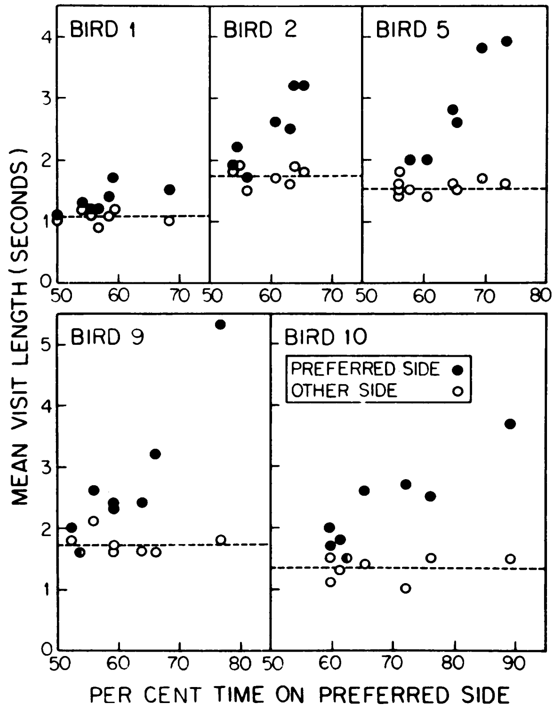

Fig. 3. Mean visit length, or stay time, on the two sides of the shuttlebox as a function of degree of preference exhibited for the last 3 days of each condition in Experiment 2. The dashed line represents the mean stay time on the less preferred side over all conditions.

preference for the 300-mg side when food came in the form of 15 small items. Unlike the cases discussed above, in this case differences in feeder times alone would tend to produce the opposite of the observed results. The 8-s feeder time for the 15 small items (vs. 1.5 s for a single small or large item) meant that large reinforcers consisting of 15 small items were effectively presented on a longer VI than large reinforcers consisting of 1 large item.

Although they spent up to 80% of their time on one side of the shuttlebox, the birds allocated their time in all the conditions so as to collect almost equal numbers of reinforcers on the two sides. When preference was close to 50:50, as in Condition 1, the average stay on either side after the COD was very short, 1 to 2 s not counting feeder times (Figure 3 and Table 3). As the total times on the two sides differed more and more, stays on the less preferred side remained minimal in length whereas stays on the preferred side increased. There was no systematic effect on changeover rate as conditions changed (Table 3).

Houston and McNamara (1981) showed that optimal performance on concurrent VIs with a signaled COD is to increase stay times on the better side as the difference between the VIs increases, while maintaining a minimal stay time on the worse side. Pigeons key pecking on concurrent VI schedules of reinforcement with food do behave in this way (Hinson & Staddon, 1983; Silberberg & Ziriax, 1982). In the present situation, maximizing rate of food intake did not require changing stay times, because the VIs on the two sides were always equal. That patterns of time allocation nevertheless changed as they did suggests a general property of behavior on concurrent VIs when the alternatives differ in reinforcing value to the animal, even if this difference is not brought about by a difference in reinforcer frequency. Silberberg and Ziriax (1982) reported a similar observation for interchangeover times in the first, equal VI links of concurrent chains.

Several previous studies of pigeons on concurrent schedules can be viewed, like the present one, as assessing whether birds value an alternative solely in proportion to the average rate of food intake it offers. For example, Todorov (1973) varied frequency and duration of grain-hopper presentation and found that frequency has a proportionately bigger effect than reinforcer duration or amount. Similarly, Schneider (1973) offered equal numbers of pellets per unit time in each of two VI components, but the food was available either in frequent small amounts or infrequent large amounts. Again, frequency was overvalued in comparison to amount. The present study complements such studies in showing that even over periods of a few seconds pigeons overvalue several small items in relation to one large one.

EXPERIMENT 3

Experiment 2 showed that when pigeons are offered equivalent amounts and frequencies of food in the form of one large or many small items, they prefer many small items, the alternative requiring longer handling time but offering more pecking. However, the conditions of Experiment 2 were highly artificial. On equal concurrent VI schedules, little or no food is lost if the animal spends slightly more time on one schedule than on another. In a natural situation, the preference for many small items over one large one would tend to lower the average rate of food intake, but perhaps the contingencies present in a natural situation would tend to override this preference. Experiment 3 was designed to see if this was so by offering choices similar to those in Experiment 2 on the shuttlebox equivalent of concurrent ratio schedules. Reinforcement on a given side was contingent on accumulating time standing on that side, and handling times did not count toward any ratio requirement. Because the required "search times" were the same on both sides, the highest rate of food intake possible in the situation could be achieved by choosing exclusively the side offering items with short handling time.

The experiment consisted of three main conditions, run with concurrent fixed cumulative duration (FCD, Shettleworth, 1975) of 10 s and a 1-s COD. In the first, one 300-mg pellet with 1.5-s feeder time was available on the left and fifteen 20-mg pellets with 8-s feeder time were available on the right. Thus the side with one large item offered a rate of energy intake about 1.5 times that on the side with many small items (26 mg/s vs. 16.7 mg/s). In the second condition the alternatives differed in E/h in the same way as in the first, but they did not differ in the amount of pecking and numbers of items they offered. One large item was available on either side, but on the left the feeder time was 8 s and on the right it was 1.5 s. The final condition was the same as the first but with the sides reversed.

In preliminary tests with various cumulative-duration schedules, the pigeons tended to fixate on one side and not to sample the other side when conditions were changed. Therefore, to make the results on successive conditions more nearly independent, blocks of "neutralization" sessions (Krebs, Kacelnik, & Taylor, 1978) were run between the main conditions. These sessions had equal progressive cumulative-duration schedules and identical reinforcers on both sides. This procedure tended to increase the rate of changing over and equalize amounts of time on the two sides for the beginning of each new main condition.

METHOD

Subjects and Apparatus

The same 5 pigeons served. Between the end of Experiment 2 and this experiment they had about 30 sessions on schedules similar to those used here. The apparatus was the same as that used in Experiment 2.

Procedure

A series of "neutralization" sessions preceded each of the main conditions. Neutralization sessions lasted 20 min, including feeder times. The feeder time was 8 s on both sides, and reinforcers consisted alternately of 1 large or 15 small pellets. At the beginning of a session, reinforcement on a given side was available after the subject had been standing on that side for 10 s. Successive reinforcers were available after $1/[.1 - .005\,(n{-}1)]$ s standing on the side, exclusive of feeder time, where n is the number of the reinforcer. The COD was 1 s. This progressive cumulative-duration schedule yielded a maximum of 20 reinforcers per side. Conditions 1 and 3 were each preceded by five neutralization sessions. Before Condition 2 there was a break of about 3 weeks after two or three neutralization sessions per bird. Therefore, extra neutralization sessions were run so that each bird had a series of five such sessions immediately preceding Condition 2.

In Conditions 1 to 3, FCD 10-s schedules were in effect for both sides of the shuttlebox throughout each 40-reinforcer session. Reinforcement was delivered each time the pigeon completed 10 s standing on a side, exclusive of feeder time. The 10 s could be interrupted by visits to the other side. The COD was 1 s. The reinforcers and handling times on the two sides have been described above and are listed in Table 4. Each bird was exposed to the conditions in numerical order for 15 sessions. Sessions were run 5 days per week.

RESULTS AND DISCUSSION

In most cases the pigeons persisted in their

Table 4

Terminal performances in Experiment 3. For the neutralization sessions (see text) means are based on the last 2 days per condition; for the main conditions of the experiment, with reinforcers and feeder times on the two sides specified in the table, means are based on the last 3 days per condition. Changeover time includes the COD (1 s) plus any additional time the bird spent in the center of the shuttlebox at the ends of CODs.

	Left reinforcer		*Right reinforcer*		*Time (s)*		*Reinforcements*		*Changeovers*		*Relative time left*
	Pellets	*s*	*Pellets*	*s*	*Left*	*Right*	*Left*	*Right*	*Number*	*Time (s)*	
Bird 1											
NEUT. 1					466.4	328.4	18	16	126	129.5	.587
COND. 1	1 × 300	1.5	15 × 20	8.0	136.6	263.5	14	26	11	13.6	.342
NEUT. 2					509.3	620.4	16	18	80	82.8	.451
COND. 2	1 × 300	8.0	1 × 300	1.5	69.2	333.4	7	33	9	10.2	.172
NEUT. 3					519.0	429.8	19	18	7	7.2	.547
COND. 3	15 × 20	8.0	1 × 300	1.5	360.0	40.7	36	4	2	4.3	.899
Bird 2											
NEUT. 1					460.8	453.6	18	18	27	29.2	.504
COND. 1	1 × 300	1.5	15 × 20	8.0	90.6	310.7	9	31	6	64.3	.226
NEUT. 2					508.4	637.5	16	18	52	54.9	.444
COND. 2	1 × 300	8.0	1 × 300	1.5	88.0	313.9	9	31	19	20.5	.219
NEUT. 3					308.1	598.0	16	19	30	31.6	.340
COND. 3	15 × 20	8.0	1 × 300	1.5	260.0	142.2	26	14	6	8.8	.647
Bird 5											
NEUT. 1					407.2	437.4	18	18	78	81.8	.482
COND. 1	1 × 300	1.5	15 × 20	8.0	242.1	160.4	24	16	30	33.6	.602
NEUT. 2					715.5	460.0	18	14	51	56.5	.609
COND. 2	1 × 300	8.0	1 × 300	1.5	68.6	334.7	7	33	7	9.1	.170
NEUT. 3					550.3	411.0	18	17	29	35.8	.572
COND. 3	15 × 20	8.0	1 × 300	1.5	200.4	204.3	20	20	6	7.0	.496
Bird 9											
NEUT. 1					366.9	550.3	16	18	26	27.6	.400
COND. 1	1 × 300	1.5	15 × 20	8.0	111.6	290.0	11	29	3	3.0	.277
NEUT. 2					546.5	663.9	16	18	11	11.0	.452
COND. 2	1 × 300	8.0	1 × 300	1.5	16.7	383.4	2	38	4	5.1	.042
NEUT. 3					646.0	312.2	20	16	11	11.0	.674
COND. 3	15 × 20	8.0	1 × 300	1.5	73.3	332.8	7	33	2	1.9	.179
Bird 10											
NEUT. 1					433.1	401.0	18	18	18	20.3	.519
COND. 1	1 × 300	1.5	15 × 20	8.0	154.6	246.8	15	25	13	13.7	.385
NEUT. 4					589.6	592.0	18	17	27	27.6	.499
COND. 2	1 × 300	8.0	1 × 300	1.5	10.0	390.0	1	39	3	4.4	.025
NEUT. 3					469.1	464.1	18	18	15	16.8	.503
COND. 3	15 × 20	8.0	1 × 300	1.5	303.9	97.7	30	10	10	8.2	.757

preference for 15 small items over 1 large one, even though under the conditions of this experiment the time spent consuming the 15 small items could have been spent reducing the time to the next large item (Figure 4). The results of Condition 2 show, however, that pigeons are sensitive to some correlate of overall rate of reinforcement in the situation used here. When identical 300-mg reinforcers were available on both sides, the birds chose overwhelmingly the side with the shorter handling time. However, when the side with longer handling time offered 15 small items, every bird increased its relative time there, although in 3 of 10 cases that relative time did not exceed 50%.

EXPERIMENT 4

One interpretation of the results of Experiments 2 and 3 is that pigeons prefer their food

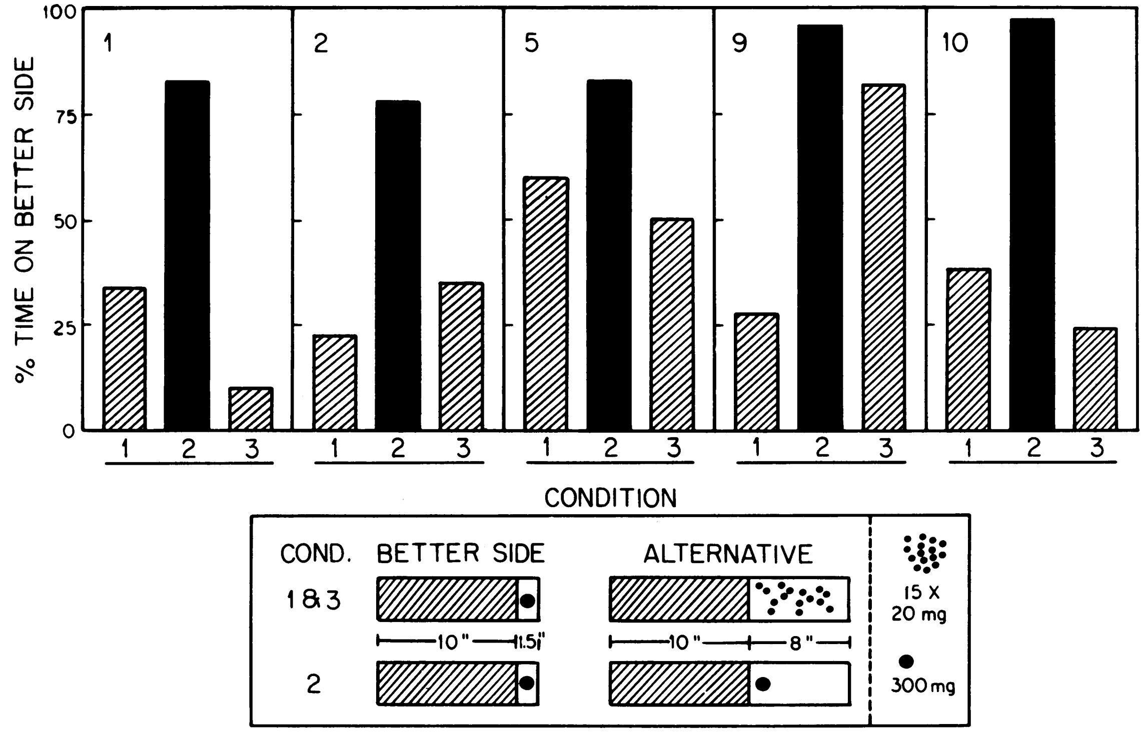

Fig. 4. Mean percentage of time spent on the side of the shuttlebox offering one large pellet with 1.5-s feeder time, the more profitable side, for the last 3 days of each main condition in Experiment 3.

in a form that affords more pecking, as if they evaluated amount of food partly by a rule of thumb, "More pecking is more food." It is also possible that the relatively large 300-mg items are somewhat aversive to pigeons. However, there are many circumstances in which they choose large items over small ones. In Experiment 2 the birds strongly preferred one large to one small item. Similarly, hungry pigeons offered a tray of large and small pellets pick out the large ones first (unpublished observations). Finally, the results of Experiments 2 and 3 are consistent with other observations mentioned earlier, which suggest that pigeons and other species overrate number of food items or feeding opportunities in comparison with size.

Experiment 4 was performed to test the generality of the pigeons' apparent preference for many, small items over fewer, larger items by offering a choice different from the 300-mg items used in Experiments 2 and 3. Concurrent VI schedules similar to those in Experiments 1 and 2 were run with one side of the shuttlebox offering four 75-mg pellets and the other side, fifteen 20-mg pellets. A shorter VI was used here to accentuate the display of a preference, which was expected to be less than that seen before inasmuch as the numbers of pellets involved in the choice differed less.

METHOD

Subjects and Apparatus

Four different 12 to 18-month-old White King pigeons served. They had previously obtained single 75-mg pellets on ratio schedules in a similar shuttlebox. The apparatus was the same as that used in Experiments 1 to 3.

Procedure

Throughout this experiment the VI schedule was 45 s. Unless specified, other aspects of the procedure were the same as those in Experiment 2. The pigeons first had five sessions of preliminary exposure to VI schedules in the shuttlebox. For these sessions, feeder times

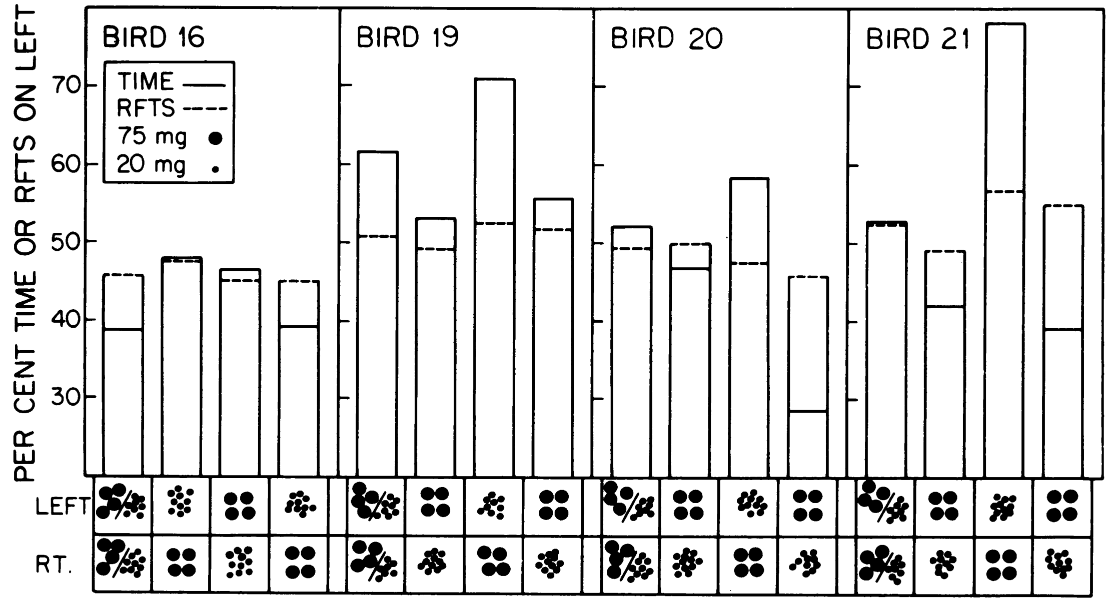

Fig. 5. Mean percentage of time spent and reinforcers obtained on the left side of the shuttlebox during the last 3 days of each condition in Experiment 4. In the key the number of small dots does not correspond exactly to the number (15) of small pellets offered.

were 5 s and reinforcers consisted of two or three pieces of pigeon chow. In the four main conditions of the experiment, reinforcers were either 20-mg ("small") or 75-mg ("medium") Noyes pigeon pellets. The latter measured 4.8 by 4 mm (diameter by height). After an initial condition in which each side of the shuttlebox offered 4 medium or 15 small pellets equally often, each bird had three conditions in which 4 medium pellets were offered on one side and 15 small on the other. In the first of these, the small pellets were on the side less preferred in the baseline condition, and the side with small pellets was switched for each successive condition. Details of the side assignments and days in each condition are provided in Table 5.

Results and Discussion

Every bird increased the relative time it spent on its initially unpreferred side when that side offered 15 small, as opposed to 4 medium, pellets (Figure 5). When sides were switched the first time, in Condition 3, the preferred side switched accordingly, and, except for Bird 16, preference switched again in the final condition. As in Experiment 2, there were considerable individual differences in degree of preference for 15 small pellets. Exact levels of preference cannot be compared across the two experiments because a shorter VI was used here. This might be expected to enhance the display of preference. However, the higher rate of food delivery on both sides might also be expected to have the opposite effect because only by staying on both sides for very short periods (and thereby keeping relative times near 50%) could the birds collect food on both sides as rapidly as it became available.

GENERAL DISCUSSION

In these experiments pigeons preferred many small items, requiring relatively long total handling time, to one or a few larger items having the same total weight but requiring less handling. This preference persisted even when it entailed a substantial cost in terms of lowering the overall rate of food intake. When handling times were equal, with single large or small items, the birds did prefer the larger item, showing, among other things, that the large items used here are not inherently aversive for pigeons. In addition, the preference for many small items over fewer larger items was evident in Experiment 4 with 15 small versus 4 medium pellets. The data do not rule out the

Table 5

Means based upon the last 3 days of each condition in Experiment 4. In all conditions the 15 small or 4 medium pellets were presented for 8 s. Changeover time includes the COD (3 s) plus any additional time the bird was in the center of the shuttlebox at the end of the COD. Times on the sides exclude feeder times.

		Pellets (Number × size in mg)		*Time (s)*		*Reinforcements*		*Changeovers*		*Relative time*
Condition	*Days*	*Left*	*Right*	*Left*	*Right*	*Left*	*Right*	*Time (s)*	*Number*	*left*
Bird 16[b]										
1	10	15 × 20	4 × 75[a]	96.2	154.6	18	22	564.2	183	.387
2[b]	15	15 × 20	4 × 75	121.1	131.8	19	21	530.2	165	.479
3[b]	15	4 × 75	15 × 20	113.8	130.7	18	22	555.9	187	.465
4[b]	20	15 × 20	4 × 75	101.2	159.2	18	22	542.3	181	.392
Bird 19										
1	10	15 × 20	4 × 75[a]	213.2	132.9	20	20	444.0	163	.616
2	15	4 × 75	15 × 20	140.3	124.0	20	20	523.0	178	.532
3	15	15 × 20	4 × 75	221.6	90.8	21	19	447.3	148	.709
4	20	4 × 75	15 × 20	145.6	116.3	21	19	498.1	164	.556
Bird 20										
1	10	15 × 20	4 × 75[a]	179.4	169.5	20	20	433.6	145	.521
2	15	4 × 75	15 × 20	169.5	193.0	20	20	426.7	156	.468
3	15	15 × 20	4 × 75	191.2	136.1	19	21	435.1	150	.584
4	20	4 × 75	15 × 20	92.2	232.2	18	22	457.3	159	.287
Bird 21										
1	10	15 × 20	4 × 75[a]	181.4	160.8	21	19	417.8	136	.529
2	15	4 × 75	15 × 20	130.5	180.6	20	20	468.2	164	.420
3	15	15 × 20	4 × 75	403.8	118.3	23	17	313.7	86	.781
4	20	4 × 75	15 × 20	141.7	220.0	22	18	394.1	129	.391

[a] alternating on both sides.
[b] side assignments different from those of other birds.

possibility that there is something intrinsically attractive to pigeons about the 20-mg "small" pellets used here. However, unpublished observations of pigeons eating simultaneously available large and small pellets in their home cages argue against this possibility, because the birds typically did not feed exclusively on the small ones and often ate only large ones. Thus the present results can best be summarized as suggesting that with successively presented collections of food items, pigeons overvalue number of items in comparison with size. As described earlier, other species are similar in this respect. The results do not permit any conclusion as to what correlate of a number of small items is responsible for their having greater reinforcing value. Possibilities mentioned previously include that many small items afford more pecking and/or other consummatory activity and have greater visual extent than one or a few larger items.

According to optimal foraging theory, if animals have evolved through maximizing net energy intake per unit time spent foraging, they should choose to feed on the most profitable items available—those with the greatest ratio of net energy to handling time—and should select these exclusively above a certain abundance. Pigeons in the present experiments did not behave in accord with this prediction. Feral pigeons of the species used here, *Columba livia*, feed largely on seeds (Murton & Westwood, 1966). Unlike, for example, nuts or insects that require extensive preparation before they can be consumed, many seeds can be snapped up with negligible handling time. Nevertheless, the whole act of fixating, pecking, and swallowing does take substantial time if performed repeatedly. Because pigeons shut their eyes when pecking and thus cannot look out for predators while grasping a seed (Zweers, 1982), they might be expected to reject food taking too much pecking time when other alternatives are available. Yet this was not the case under the conditions of the present experiments.

Do pigeons, then, behave suboptimally? Before concluding that they do, some other possibilities need to be explored. First, there may be some hidden cost of ingesting large as opposed to small items, such that many small items give a greater net energy yield than an equal weight of large items. This possibility could be investigated by giving pigeons diets composed entirely of large or of small items. Even if many small items are less profitable than fewer larger items over periods of hours or days, as has been assumed throughout this paper, the small items may be digested more rapidly by a hungry pigeon. Food ingested by pigeons and similar birds may be held in the crop for up to 24 hours. There it is softened by mucous secretions but is not digested until it passes on to the glandular stomach and thence to the gizzard (Ziswiler & Farner, 1972). Thus digestion would normally occur hours after ingestion. If the crop is empty, however, as it probably would be in birds not fed for 23 hours, food passes out of it immediately. Thus it is possible that for hungry birds, choice of small items over large would be correlated with quicker physiological effects of the food. Note, however, that the particular food used here crumbles into a coarse powder almost as soon as it is moistened. It therefore seems unlikely that the birds acquired a preference for small items in the course of the experiments on the basis of the rate at which they were digested. Rather, if small items are more quickly or efficiently digested than large ones in general, the kind of rule of thumb that was observed to describe the birds' behavior would tend to evolve.

Finally, the pigeon's mechanism for selecting food items may be more nearly optimal in natural situations with many different sorts of items available simultaneously than in the artificial situation used here where the alternatives are discrete collections of items presented successively. As has already been noted, caged, food-deprived pigeons presented with an array of the same small and large items used in Experiments 1 to 3 do not eat all the small ones but rather select the large ones first.

The obvious parallels between foraging and behavior on schedules of reinforcement have inspired a number of studies using pigeons to investigate whether optimal selection among food items can be accounted for by known properties of food-reinforced behavior. In the simulation pioneered by Lea (1979), handling time is equated to the delay to availability of food reinforcers of fixed quantity. As predicted by optimal foraging theory, acceptance of less profitable "items" (e.g., tendency to peck a key signaling the longer of two delays) depends on frequency with which the more profitable items are available. It appears that the results from these simulations can be encompassed by the same delay-reduction principle that accounts for behavior in conventional concurrent chains (Abarca & Fantino, 1982).

The present results, however, suggest some caution in designing laboratory simulations of foraging problems based on their formal properties alone. In Lea's (1979) simulation, any deviation from optimality was in the direction of too-ready rejection of the "unprofitable," long-delay (hence, long "handling time"), alternative. The present results suggest that in choosing among real food items, pigeons would show the opposite bias, tending to accept an unprofitable collection of small items too readily, despite this longer total handling time. Thus the events that compose a "handling time" may be of crucial importance. Snyderman's (1983) data make a similar point in showing that relative lengths of prefood and postfood delays within a constant "handling time" alter simulated item selection. Because animals do not literally optimize but rather approximate in making their choices, as described by simple rules of thumb (Hinson & Staddon, 1983; Krebs et al., 1983), these differences in behavior in formally identical situations are to be expected. It might be suggested that one purpose of psychological research on foraging should be to understand what these rules of thumb are (cf. Snyderman, 1983). In the present case, this means trying to identify the dimensions of food the pigeons are critically sensitive to in different situations. Clearly, laboratory studies analyzing foraging must take into account all the factors present in natural foraging situations, some of which are not yet incorporated in formal models of foraging or schedule behavior.

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